Thermal and Salinity Effects on Ciliary Activity of Excised Gill Tissue from Bivalves of North and South Carolina

BY

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(4 Text figures)

INTRODUCTION

In the study of the distribution of marine animals, whether molluscan or of any other group, it was found that temperature and salinity have a pronounced effect on the animal (Gunter, 1957; Schlieper & Kowalsky, 1956a, 1956b). Similarly, substrate can have a marked effect on the distribution within the species' range (Bird, 1970).

In the past, most studies have emphasized the effect of temperature and salinity on the whole animal (Hoar & Robertson, 1959, on fish; Peiss & Field, 1950, on fish; Wells, 1961, on mollusks; McLeese, 1956, on lobsters). Whole organism studies, however, were not always reliable for mollusks because a whole animal response to tactile stimulation is used and a recovery period is necessary. Sublethal damage to bivalves would go unobserved and affect later tests if the same individuals were used again. Henderson (1929) subjected intact bivalves directly to water baths at constant temperatures and measured the temperatures needed to cause continued gaping of the valves after the mantle was touched with forceps. However, species which lock shut upon death would be useless here, as would measurement of autolysis or partial recovery of ciliary movement prior to death. Later, use of isolated gill tissue from bivalves was adopted to derive exact thermal and temporal determinations of ciliary responses (Schlieper, 1951, 1958; Vernberg *et al.*, 1963).

After collecting numerous mollusks in deep water on reefs off South Carolina, little information in the literature was found on physical tolerances of marine epibenthic bivalves. Since these reefs were just recently described (Menzies *et al.*, 1966), analysis of molluscan assemblages was still sketchy. While *Arca zebra* and *A. imbricata* have been recorded for many years in Carolina waters, popular references do little to clarify where these bivalves even occur, let alone thermal and salinity resistance (Abbott, 1954, 1963, 1968; Barrett & Patterson, 1957; Johnston, 1957). All that was said in such typical sources was that the bivalves were very common in shallow water. Since *A. imbricata* is found in from 15 - 25 m of water in Carolina waters and *A. zebra* down to 40 m, none of these sources is of much value in describing the distribution of these populations.

Recent studies by Stanley (1970) do little to shed light on the substrate preference or physiological tolerances of these bivalves. *Arca* populations studied by him were from south Florida and although both species were found in only 1 or 2 m of water, no habitat difference between the two species was discerned. Other studies of more southern populations (Houbrick, 1968) report the same shallow depth utilized by *Arca* populations in Florida. Other epibenthic bivalves, *Mytilus edulis* Linnaeus, 1758 and *M. californianus* Conrad, 1837, have been noted living together in California waters (Harger, 1968a, 1968b, 1970). However, the ability of the byssus of these two species to withstand wave impact is the factor separating their niches. While the byssus of *A. imbricata* is proportionally larger than that of *A. zebra*, thermal tolerances would probably be more important in separating *A. zebra* and *A. imbricata* since wave effect is unimportant for northern populations in deep water.

NATURAL HISTORY

Arca zebra, A. imbricata, and *Chione cancellata* were chosen for this study because of the similarity in their modes of life. All three have the same geographical range and each is the dominant epibenthic bivalve in its habitat. Popular references (Abbott, 1954, 1968; Warmke & Abbott, 1963) describe *A. zebra* and *A. imbricata* as living attached to rocks in shallow water from North Carolina to the Lesser Antilles and Brazil. *Chione cancellata* is found in shallow water of the Southeast United States and West Indies. Reportedly, they are all common along their entire range. While this may be true in the West Indies and south Florida, northern researchers would find these comments on distribution somewhat misleading.

Arca zebra Swainson, 1883

Arca zebra, the largest of the three species, averages 3 inches (7½ cm) in length. It has a thick, strong shell twice as long as wide. Numerous brown zebra-like stripes cover the exterior, and growing over most of the outer shell is a shaggy green periostracum which partially disguises the tell-tale stripes. For further camouflage, *A. zebra* is covered with encrusting corals, sponges, bryozoans, tunicates, algae, and the herbivorous gastropods *Crepidula acuiformis* (Gmelin, 1791) and *Crucibulum striatum* Say, 1826. The inside of this bivalve is a dull purplish brown.

Arca zebra grows firmly attached to hard substrates. The foot produces a shiny, olive green byssal clump, short but strong, which protrudes through a byssal gape in the ventral edge of the shell. This gape is an opening along the middle of the valves and faces directly on the substrate selected for attachment. This surface to which it attaches may be rock, compressed shell, another shell of *Arca,* other bivalves, sponge, or soft coral. The animal is so firmly attached that only a concerted effort of much pulling and twisting will dislodge it; often the byssal clump is pulled completely out of the foot and remains on the substrate. Commonly, the sponge or bryozoan substrate later surrounds the animal, leaving only its dorsal hinge area exposed.

Arca zebra is reputed to be very common in shallow water. Warmke & Abbott (1963) describe it in Puerto Rico as living attached to rocks in only a few feet of water. Beaches of south Florida and the Florida Keys are littered with dead shells after storms, attesting to the shallow depths preferred in this part of their range. Observations in shallow water along the Carolina-Georgia coast, however, indicate it is completely absent and only extensive dredgings revealed the true habitat of northern populations. As a result of dredging from the R/V *Eastward,* this species was located on reefs which extend from Charleston, South Carolina to Onslow Bay and Lookout Shoals, North Carolina, offshore 15 to 50 miles (24 to 80 km). The reefs on which *A. zebra* live occur under the Gulf Stream in 25 to 40 m of water and can be visually located on the ship's depth recorder. Typically, they appear as large, rounded or jagged humps arising from the ocean floor. However, certain flat and bare reefs, undetectable on the depth recorder, may be adequate for attachment. Although *A. zebra* may occur in depths as shallow as 15 m, these populations are represented by only a few small, scattered individuals.

However, at any depth, bare rock alone is not sufficient for attachment. *Arca zebra* and *A. imbricata* occur only on those portions of reef which also support thick growths of coral and sponge. Apparently the Gulf Stream and its accompanying current and warm temperature may help keep an optimal level of food and sediment in the water column.

Arca imbricata Bruguière, 1789

Many of the comments concerning *Arca zebra* can also be applied to *A. imbricata.* Although having the same general shape, *A. imbricata* is slightly smaller, averaging 2 inches (5 cm) in length, thicker, fatter, with no stripes. As it reaches its maximum depth of 25 m, however, it is almost as large as the deeper occurring *A. zebra* and covered with the same green colored periostracum as found on *A. zebra.* The byssus is similar to that of *A. zebra* and attaches in the same manner.

Arca imbricata occurs on reefs and rocky surfaces, a habitat similar to that favored by *A. zebra.* Reefs with large populations were found in Onslow Bay and Lookout Shoals, North Carolina. Depth, however, seemed to be the obvious factor separating these two species. *Arca imbricata* was found in North Carolina in 15 to 17 m of water and extended to 25 m. The largest individuals of *A. imbricata* come from the deepest limit of their distribution where *A. zebra* begins to assume dominance. At the overlapping depth of approximately 25 m, *A. zebra* populations are composed of small individuals, but as soon as *A. imbricata* disappears, *A. zebra* assumes its normal size down to its maximum depth of 40 m, where only stunted individuals occur.

While *Arca imbricata* were collected in greatest numbers on North Carolina reefs in 15 - 25 m of water, this does not necessarily mean that they do not occur in shallower water. I have seen specimens collected from the beaches near Myrtle Beach, South Carolina, with valves still intact. This species, therefore, may be able to live in much shallower water if suitable surfaces for attachment occur. While inshore reefs are not commonly found off South Carolina, isolated rocky outcroppings or wrecks may provide suitable surfaces for these animals to establish themselves.

Chione cancellata Linnaeus, 1758

Chione cancellata is the shallowest occurring of the 3 species discussed, with the same geographical range as *Arca zebra* and *A. imbricata,* occurring from North Carolina to the West Indies. However, literature searches (Abbott, 1954, 1968) yield little information on substrate preference. In these and other sources, typical habitat is described as "common in shallow water" and "abundant in brackish water." This gives little preliminary aid in collecting large numbers of individuals for laboratory research. Substrate reference resulting from extensive dredging will be discussed later in "Results."

METHODS AND MATERIAL

General Care

These three species were chosen because of the similarity in their modes of life. All three are essentially nonmotile bivalves living on the surface of the bottom. *Arca zebra,* a deep water species, and *A. imbricata,* a medium depth species, were obtained in offshore waters of North and South Carolina by dragging a Cerame-Vivas rock dredge for half an hour across reefs of coral and rock, with the animals collected in a trailing chain mesh bag. The living animals were removed and kept aboard ship for several days in large aerated containers until the bivalves could be brought to the laboratory. Here they were scrubbed clean of all encrusting organisms to eliminate fouling and kept in a 100-gallon (360 l) capacity, temperature-controlled tank. Animals tested at ambient temperatures were used immediately, and other animals were temperature acclimated for at least 2 weeks. *Chione cancellata* was gathered with a homemade dredge of a design similar to that of the Cerame-Vivas dredge but proportionally smaller. The dredging time was only 5 or 10 minutes since the area to be sampled was much smaller. These animals were brought back to the laboratory the same day and placed directly in the holding tanks. *Chione cancellata* was seldom encrusted and required little cleaning. Those animals to be tested at ambient temperatures were also used within a week, while individuals to be acclimated were stored in a separate aquarium.

The salinity averaged 32‰ in both holding tanks, even though unfiltered sea water was periodically added to make up for evaporation. Although food matter and algae may have been present in the tanks and added water, these animals were essentially starved.

Half the animals captured were kept at the same temperature as the bottom from which they came. These individuals were tested after 2 days in the laboratory to allow for recovery from the shock of collection. When possible, animals were tested in 2 temperature baths simultaneously in groups of 4 or more.

Those animals dredged in the summer at 17 - 21° C were considered warm-acclimated. Therefore, the individuals to be cold-acclimated were exposed to water of 10° C. Animals coming from 9 - 10° C water were considered cold-acclimated and those to be warm-acclimated were subjected to 20° C for the 2-week acclimation period.

Preparation of Gill Tissue

The cilia on the bivalve's gills are rapidly beating hairlike structures at the end of the gill filament. These are easily seen under the high-power microscope and their rate of death and autolysis is easily predicted once the basic thermal tolerance has been determined. Most bivalve cilia of the same species stop beating at nearly the same temperature.

Previous studies (Henderson, 1932) have used the whole animal in thermal determinations, but here the exact time of death is in doubt. The researcher had to base his judgment on the time required before the two valves would open and not close again upon tactile stimulation. *Chione cancellata,* at death, does not always open but rather closes tightly, as do many other bivalves, rendering this approach useless.

To obtain the gill tissue, the bivalves were gently broken open with a hammer. With the body still intact, the gill

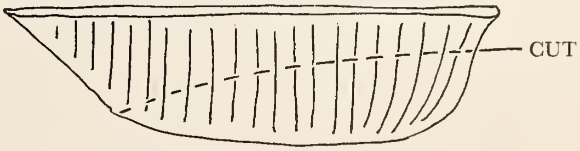

Figure 1

Diagrammatic view of gill tissue with the portion to be used indicated by dashed line (CUT) tissue was easily dissected from the other tissues and placed in a Petri dish of filtered sea water. Since the ventral half of the gill tissue contained the distal edge of the filament with cilia, and the entire gill filament was too long to fit on a microscope slide, the dorsal half of the filament was cut away and discarded (Figure 1). Then the tissue was easily cut into 3 mm sections, each containing many filaments with hundreds of cilia.

Cilia

The cilia used were terminal (Figure 2). *Arca zebra* and *A. imbricata* also have cilia on the sides of the gill filaments, but these have little thermal resistance. Only the middle section of the gill tissue was used because towards the end of the gill, the cilia and filament decrease in size and are too small to be observed accurately. *Chione cancellata* also has lateral cilia but only in small numbers. These cilia occur in clumps and are also more sensitive than terminal cilia.

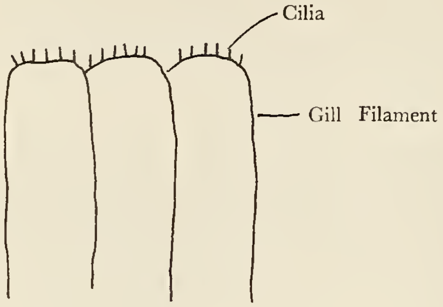

Figure 2

Terminal cilia on the end of gill filament sections

Whenever possible, separate gill pieces from one animal were subjected to several different water baths. Single individuals of *Arca zebra* and *A. imbricata* had enough gill sections available after dissection to allow 3 separate temperature or salinity tests being run simultaneously. *Chione cancellata*, on the other hand, was too small for more than one test per individual, and for longer periods of time, sections from 2 individuals of *C. cancellata* had to be placed in the same flask.

To test thermal resistance, the cilia were heated or cooled in a water bath. Stoppered flasks of filtered sea water were allowed at least 30 minutes to equilibrate with the water bath. Thermometers, accurate to 1/10 of one degree, were used to check both flask and water bath temperatures periodically to insure constant temperature. A large-bore pipette was used to transfer the gill sections from the Petri dish to the flask, care being taken to add as little water as possible to avoid unnecessary temperature change. Every 15 minutes one gill section was removed from each flask, placed on a microscope slide and covered with a coverslip. For thicker filaments, such as those of *Chione cancellata,* a depression slide was used, as the coverslip on a regular slide crushed the gill section. Under the high-power microscope (400×), the terminal cilia were easily visible and the rate of activity decrease was clearly discernible. The corresponding increase in autolysis was equally visible.

The activity chart (Table 1) was used to rate the decrease in movement of the cilia. Although some degree of subjectivity in the observation was evident, these levels of activity were easily separated.

Table 1

Activity Chart Used to Rate the Activity of Cilia from the Terminal End of Bivalve Gill Filaments

3 – Normal Activity
2 – Somewhat Reduced Activity
1 – Greatly Reduced Activity
0 – No Activity

Under the microscope, the terminal cilia appeared as a blur when beating at a normal rate of Activity 3. This beating was strong enough to create a current which could carry observed alga cells along its border. During decreases in activity, the cell began to lose cytoplasm from between its filaments. Activity 2 had only 75% of the cilia capable of movement, with each cilium readily visible. Autolysis then began, with cytoplasm exuding into the water medium. Activity 1 had only 10% of the cilia beating, quite slowly to barely a flicker. Cytoplasm and organelles covered the margins of the cells, with visibility of the cells becoming difficult at times. At rate 0, the cilia stopped beating entirely and the margin of the cell was barely discernible. Only upon introduction of the gill sections into the highest temperature water baths, where the gill sections lived less than 15 minutes, did the cell not rupture. Here, the cell appeared to go into a state of shock.

Thermal Resistance

The thermal resistance of gill tissue was determined as a function of time versus temperature. The gill sections awaiting testing in the Petri dishes were kept in sea water from the same container in which the animal lived to keep thermal and physiological changes to a minimum prior to being placed in the experimental flask. To hold the gill sections, stoppered Erlenmeyer flasks, filled with filtered sea water of 30‰ salinity, were suspended in a temperature-controlled water bath. These flasks were allowed at least 30 minutes to equilibrate after the bath had reached the desired temperature. To prevent mistakes in the time interval between observations, gill sections were placed in the flask only at intervals of 0, 15, 30, or 45 minutes past the hour. These sections were transferred as rapidly as possible to the flask to prevent temperature change.

The flask itself was filled to within one inch ($2\frac{1}{2}$ cm) of the top to keep temperature fluctuations to a minimum. Only one animal's gill section was included in each flask, except in the case of prolonged exposure for *Chione cancellata* where several individual's gill sections were kept together in one flask. At no time did the temperature drop more than 0.5° C, and seldom more than 0.1° C. After removal with a large-bore dropper, the gill sections were placed under a cover slip on a microscope slide, regular or depression (see above), and observed under the compound microscope, using the oil immersion objective.

In seeking the thermal tolerances, both upper and lower lethal limits were examined. Cilia were checked once every 15 minutes until Activity 0 was reached. This was continued for all species which could survive over 15 minutes at any given temperature. When the critical temperature was attained in less than 15 minutes, the cilia were checked every 5 minutes. When no activity was observed, regardless of time period, a second gill section was checked to exclude any individual tissue variation or dissection damage to the tissue.

At lower lethal limits, temperatures were checked every 15 minutes, as before, for up to 180 minutes. These levels were then decreased in 1° C intervals until −1° C was reached. Presumably, if the water temperature were lowered to freezing, −2° C, the gill sections would cease activity and die. Since this is an unnatural occurrence, natural conditions seldom going below 9° C, this low level was deemed unnecessary for this experiment.

Osmotic Resistance

Cellular osmotic resistance was measured by exposing gill tissue to various salinities. To cover the estuarine range, 15‰ and 25‰ were used for *Arca zebra* and *A. imbricata,* with 35‰ used as the control. For the more euryhaline *Chione cancellata,* the lower salinities acted as a control and 35‰ as the abnormal exposure. Ten or 12 sections were rinsed in distilled water and placed in a temperature-controlled refrigeration container. The temperatures tested were 10°, 25°, and 35° C for both natural (field) and acclimated individuals. The activity of the cilia was then observed at the following intervals: $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$, 1, 2, 3, 4, 6, 12, 24, 48, and 72 hours. The salinities were measured with a refractometer since the salinity interval was fairly large and easily readable.

RESULTS

Osmotic Resistance

The osmotic resistance was determined by observing the ciliary activity at predetermined time intervals up to 72 hours. Each salinity measurement at each temperature was tested with 3 individuals of each species, both acclimated and ambient.

Gill cilia from all 3 species showed no difference in their ability to withstand abnormal salinity, whether raised, in the case of *Chione cancellata,* or lowered for *Arca zebra* and *A. imbricata.* Neither did thermal acclimation change the ciliary response to the unnatural salinity levels. Lower salinities were not deemed necessary, since these were far lower for *A. zebra* and *A. imbricata* than would ever occur in nature. While salinity on the reefs offshore does reach 29‰, nothing approaching 15‰ is probable. Similarly, while salinity has been noted at 10‰ in the area where *C. cancellata* was collected, these determinations were made from the surface and do not reflect epibenthic values which would probably be higher. Since *C. cancellata* does not occur littorally or in burrows, greatly reduced salinities do not occur.

Thermal Resistance

Data representing the length of time terminal cilia of both ambient and acclimated individuals of all 3 species can withstand upper maximum temperatures are presented in Table 2.

Both *Arca zebra* and *A. imbricata* showed no ability to acclimate, with values being equal for all temperatures. Since there was no possibility in this portion of their range for rapid daily or seasonal changes, the inability to acclimate was expected. At the lowest temperatures, sublethal damage only was done to the gill cilia, the activity rate being no lower than 2 when the experiment ended.

Table 2

Thermal Resistance Time at Elevated Temperatures (in minutes) of Isolated Gill Tissue of Bivalves

Temperature	Cold-Acclimated (10° C)		Warm-Acclimated (20° C)	
	Mean Time and Standard Error of the Mean	Range and Number of Determinations	Mean Time and Standard Error of the Mean	Range and Number of Determinations
		Arca zebra		
41	13.0 ± 1.09	10 - 15 (5)	13.0 ± 1.09	10 - 15 (5)
40	38.3 ± 2.47	30 - 45 (9)	37.5 ± 2.7	10 - 15 (5)
39	62.8 ± 2.92	30 - 75 (16)	64.5 ± 2.5	45 - 75 (14)
38	194.3 ± 1.0	165 - 210 (7)	195.0 ± 3.6	180 - 210 (19)
37	over 180	- (5)	over 180	- (5)
		Arca imbricata		
43	15.0 -	- (4)	15.0 -	- (5)
42	57 ± 1.71	30 - 60 (20)	60.5 ± 2.1	30 - 75 (17)
41	102.5 ± 2.53	90 - 105 (11)	102.5 ± 2.53	75 - 105 (11)
40	over 240	- (5)	over 240	- (5)
		Chione cancellata		
42	under 5 -	5 (5)	under 5 -	5 (5)
41	15.0 ± 1.09	10 - 15 (5)	15.0 -	15 (15)
40	37.5 ± 2.47	30 - 45 (10)	43.9 ± 2.34	15 - 60 (14)
39	75.0 ± 2.92	45 - 105 (15)	90.3 ± 4.55	45 - 120 (19)
38	156.0 ± 10.9	120 - 165 (5)	165.0 ± 1.0	105 - 210 (7)
37	over 210	- (5)	over 210	- (5)

The shallow water *Chione cancellata* did show some degree of acclimation. Since these are all estuarine individuals, slight acclimation was to be expected. At lower temperatures, 2 or more individuals were used in each flask. At 37° C the activity rate was still 3, even after 210 minutes. Occasionally, one individual's gill cilia would stop beating sooner than others', as reflected in the range. While outwardly healthy in appearance, these cilia would cease activity at temperatures lower than expected. Individuals of all species, regardless of acclimation, often would increase the level of activity just prior to death. From an activity of 1, they would suddenly increase to Activity 2 and then permanently cease ciliary movement. Figures 3 and 4 show the upper lethal limit of all 3 species in graphic form.

Low temperature experiments all showed normal activity for all species, regardless of acclimation. To prevent freezing at 0° and −1° C, methyl and isopropyl alcohol were added to the water bath. At all temperatures, from +5° down to −1° C, 5 individuals of each species were used. Even at these low temperatures, well below experienced field conditions for any of these 3 species, no reduction of ciliary activity was observed. All ciliary activity after 180 minutes was still at Activity 3.

Chione cancellata

Extensive inshore dredging revealed that this species is not very common, although general accounts in popular references state that it is a very abundant species. Benthic samples taken throughout the North Inlet Estuary, South Carolina, in an attempt to locate suitable populations of *Chione cancellata* for laboratory research, indicated that this species preferred a substrate very limited in geographical distribution. Most of the wider creeks draining into North Inlet have sandy bottoms or, in regions of very little current, mud bottoms. Both these substrates proved to be devoid of this bivalve species. Only deeply scoured areas, or regions with strong currents and hard shell bottoms, yielded large populations. Associated organisms, such as crabs, echinoderms, and subtidal oysters, were also much more abundant in these areas. In the area known as Clambank Creek, over 99% of the epibenthic bivalves were *C. cancellata. Chione cancellata* was not attached but simply lay on the bottom.

To compare this finding of limited substrate preference, similar dredgings were also made in Murrel's Inlet, South Carolina. Samples were taken from all the larger creeks leading into the inlet and throughout the inlet itself.

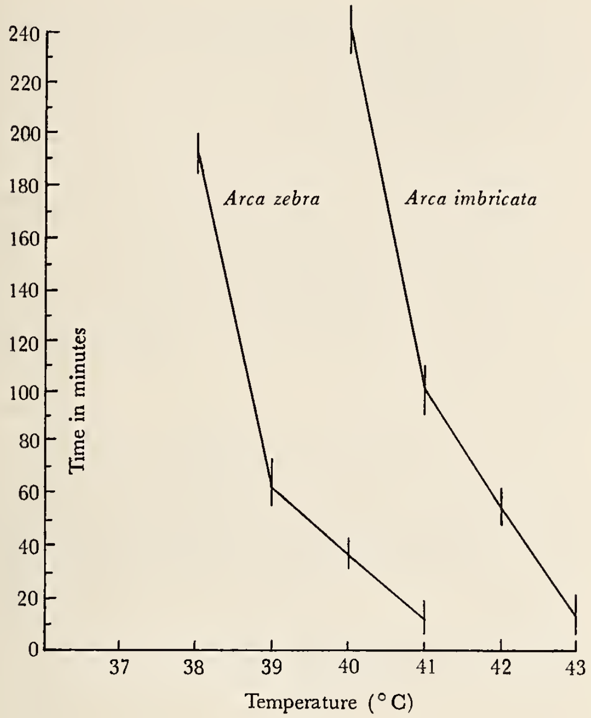

Figure 3

Upper lethal limits (in minutes) of gill cilia from warm- and cold-acclimated *Arca zebra* and *Arca imbricata*

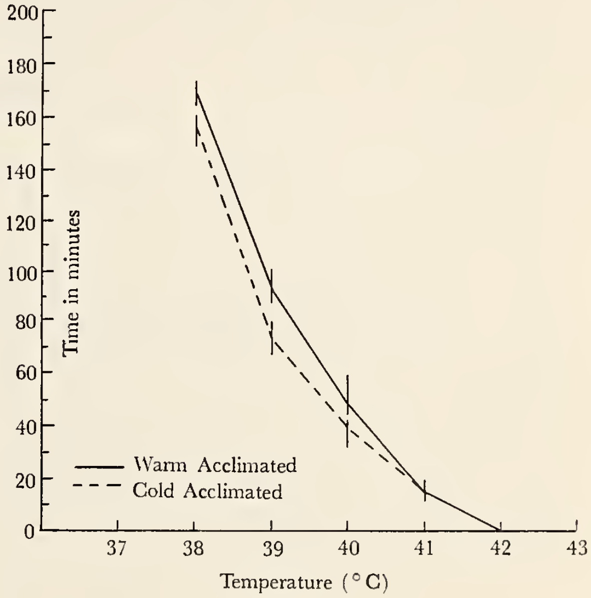

Figure 4

Upper lethal limits (in minutes) of gill cilia from warm- and cold-acclimated *Chione cancellata*

Only at locations with sufficient current to keep sediment deposition to a minimum was *Chione cancellata* found. This species was absent in inflowing creeks, all of which had mud bottoms, and throughout the inlet itself where the bottom was composed of sand. Only in that portion of the inlet where the main creeks join, the bottom being composed of oyster shell and hard mud, was *C. cancellata* common. Here it was found abundantly, as were many associated organisms.

CONCLUSIONS

In North and South Carolina, *Arca zebra* and *A. imbricata* were found only in offshore waters under the Gulf Stream where suitable reef sites occur. Both *A. zebra* and *A. imbricata* represent the most dominant epibenthic bivalve of their respective communities. *Arca zebra* does not live above 25 m, while *A. imbricata* can be found in water 15 to 25 m deep, but can probably live in shallower water if suitable substrates exist.

Arca imbricata, although smaller, has greater resistance to thermal stress than does *A. zebra.*

Chione cancellata has the same latitudinal range as *Arca zebra* and *A. imbricata* and is by far the most dominant epibenthic bivalve on its specialized substrate of hard shell, strong currents, and little sedimentation. Its estuarine distribution in the northern portion of the range does not overlap that of *A. zebra* or that of *A. imbricata.*

None of the cilia of these 3 species showed any response to altered salinities (15, 25, and 35‰) and after 72 hours the cilia moved at normal speed at temperatures of 10°, 25°, and 35° C.

Arca zebra and *Chione cancellata* are less heat tolerant than *A. imbricata,* ceasing ciliary activity 2° C lower than *A. imbricata.*

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